

OBSERVATIONS ON THE GENUS *PLAGIOSELMIS* (CRYPTOPHYCEAE)

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ABSTRACT - The description of the genus *Plagioselmis* Butcher (Cryptophyceae) is emended based upon the type species, *Plagioselmis prolunga* sp. nov., *P. prolunga* var. *nordica* var. nov., and *P. nannoplanctica* (Skuja) comb. et stat. nov. The genus belongs to the order Cryptomonadales Novarino et Lucas owing to the fact that the nucleomorph is positioned outside the pyrenoid. The principal feature of the genus is given by the presence of a tail, a posterior appendage lacking the discrete hexagonal periplast areas found on the main portion of the cell body. Taxa of *Plagioselmis* can be distinguished from one another based upon the presence or absence of a ventral sulcus, relative flagellar length, presence or absence of body scales, position of the pyrenoid and nucleus, chloroplast shape, cell size, size of the periplast areas, contents of the tail, and habitat. *Plagioselmis prolunga* contains phycoerythrin I, as does *P. nannoplanctica*. The phycocyanin-containing species *Chroomonas acuta* Utermöhl may belong to the genus *Plagioselmis*, since published SEM micrographs have shown that it possesses the tail typical of the genus. The status of the genus *Isoselmis* Butcher, originally described as being similar to *Plagioselmis*, is uncertain and the generic name *Isoselmis* may represent a nomen dubium which cannot be applied to any taxon.

RÉSUMÉ - Le genre *Plagioselmis* (Cryptophycées) est redécrit à partir d'observations effectuées sur *Plagioselmis prolunga* sp. nov. (espèce-type), *P. prolunga* var. *nordica* var. nov., et *P. nannoplanctica* (Skuja) comb. et stat. nov.. Le genre appartient à l'ordre des Cryptomonadales Novarino et Lucas, caractérisé par la position du nucléomorphe (à l'extérieur du pyrénéoïde). La caractéristique principale du genre est donnée par la présence d'une queue postérieure, dont le périplaste est dépourvu des aires hexagonales présentes dans la région principale du corps cellulaire. Les taxons de *Plagioselmis* se distinguent l'un de l'autre par la présence ou absence d'un sulcus ventral, la longueur relative des flagelles, la présence ou absence d'écaillies sur le corps cellulaire, la position du pyrénéoïde et du noyau, la morphologie du chloroplaste, la taille des cellules et des aires du périplaste, le contenu de la queue, et l'habitat. *Plagioselmis prolunga* et *P. nannoplanctica* contiennent comme pigment accessoire la phycoérythrine I. La cryptomonadine à phycocyanine *Chroomonas acuta* Utermöhl pourrait appartenir au genre *Plagioselmis*, car des micrographies au MEB disponibles dans la littérature ont montré que cette espèce possède la queue typique de *Plagioselmis*. Le genre *Isoselmis* Butcher, décrit par son auteur comme étant semblable à *Plagioselmis*, est à qualifier de 'douteux'.

KEY WORDS: Cryptomonads, Cryptophyceae, fine-structure, *Plagioselmis nannoplanctica* comb. et stat. nov., *Plagioselmis prolunga* sp. nov., *Plagioselmis prolunga* var. *nordica* var. nov., taxonomy.

INTRODUCTION

The genus *Plagioselmis* (Cryptophyceae) was described by Butcher (1967), together with another genus (*Isoselmis*) which Butcher considered as being closely allied to *Plagioselmis*. Butcher based the genus *Plagioselmis* on two phycoerythrin-containing marine species, *P. prolunga* Butcher and *P. punctata* Butcher. He omitted to designate a type species, but this was indicated by Chrétiennot-Dinet (1990) as *P. prolunga*. Since the original description of *Plagioselmis*, there have been only few reports of cryptomonads identified as belonging to that genus (Chang, 1983; Thronsen, 1983; Thronsen & Kristiansen, 1988; Novarino, 1991b; Hill, 1992; Kuylenstierna & Karlson, 1994). Although some information is available on the nucleomorph (Morrall & Greenwood, 1982), the phycoerythrin pigment (Hill & Rowan, 1989), the periplast (Novarino, 1991b; Kuylenstierna & Karlson, 1994), and the morphology of the vestibular region from which the flagella arise (Hill, 1992; Kuylenstierna & Karlson, 1994), *Plagioselmis* is among the least known genera of cryptomonads, and information on its fine-structure and species-level taxonomy is as yet unavailable.

Very few culture strains of *Plagioselmis* are available at present. Butcher (1967) based his *P. punctata* on strain no. 172 from the Plymouth Culture Collection, U. K. (PLY), which had been isolated by Mary Parke in 1957 from St Germain's River, U. K.. That strain is no longer listed in the Plymouth collection catalogue, but there is a more recent one which also bears the name *P. punctata* Butcher. This strain (no. 172a) was isolated by R. Jowett in 1969 from the type-locality of *P. punctata*; it was included in fine-structural studies by Morrall (1980) and Morrall & Greenwood (1982). A study by Hill & Rowan (1989) lists a strain named *P. prolunga* Butcher from Melbourne University Culture Collection (MUCC no. Cr011).

We have examined strain PLY 172a and carried out further observations on specimens from the North Sea plankton previously identified as *Plagioselmis* sp. (Novarino, 1991b). We have also examined a freshwater strain previously identified as belonging to the genus *Rhodomonas* Karsten. As a result, the diagnosis of the genus *Plagioselmis* is emended; Butcher's diagnosis of *Plagioselmis prolunga* is validated by designating a lectotype; a new variety and a new combination in the genus *Plagioselmis* are described, and the possibility is discussed that *Chroomonas acuta* Utermöhl may belong to the genus *Plagioselmis*.

MATERIAL AND METHODS

Light and electron microscopical observations were carried out on the marine strain no. 172a from the Plymouth Culture Collection, U. K. (PLY), listed in the collection catalogue as *P. punctata* Butcher; and the freshwater strain no. N750301 from the collection of Dr Dag Klaveness, University of Oslo (DK), originally named *Rhodomonas lacustris* (Pascher et Ruttner) Javornicky (Klaveness, 1981). Cultures were maintained as described by Morrall (1980) and Novarino (1991a, b). For light microscopy (LM), it was necessary to fix the rapidly swimming cells with Lugol's iodine. Observations were carried out using bright-field and phase-contrast Zeiss Neofluar and planapochromatic objectives (x40 and x100).

For scanning electron microscopy (SEM), strain PLY 172a was prepared and observed as described by Novarino (1991a), except that the fixation schedule was preceded by a pre-fixation step (3 additions of 10 drops of buffered glutaraldehyde to 15 ml of uncentrifuged culture over a period of 30 mins); strain DK N750301 was prepared as described elsewhere for *Cryptomonas marssonii* (Novarino, 1991b). Measurements of whole cells and periplast areas were taken as described by Novarino (1991a, b) and Novarino & Lucas (1993a).

For transmission electron microscopy (TEM), strain PLY 172a was prepared and observed as described by Morrall & Greenwood (1982); strain DK N750301 could not be fixed satisfactorily for TEM, but information on the internal cell structure of this strain is available from a study by Klaveness (1981).

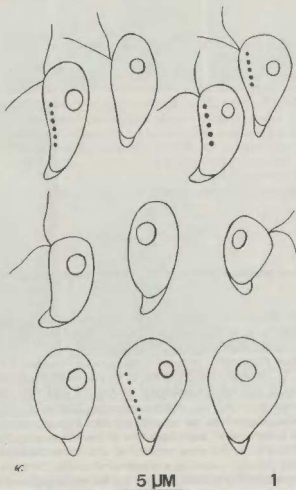


Fig. 1. Lugol-fixed cells of *Plagioselmis prolonga* PLY 172a as seen with the LM. Note the anterior pyrenoid and the posterior hyaline tail.

Further observations were carried out on *Plagioselmis* sp. from the North Sea plankton, prepared and observed as described by Novarino (1991b).

The phycoerythrin pigment of strain PLY 172a was extracted and characterized using a standard procedure (see Novarino & Lucas, 1993a).

ABBREVIATIONS

The following abbreviations are used in the text: CPD = critical point-drying, IPC = internal periplast component, LM = light microscope, PAs = periplast areas, PM = plasma membrane, SEM = scanning electron microscope, TEM = transmission electron microscope.

TAXONOMY

Plagioselmis Butcher emend. Novarino, Lucas et Morrall

Description: Cryptomonadales Novarino & Lucas 1993b (non Cryptomonadales Pascher nec Cryptomonadales auctorum). Cells with apically or subapically attached flagella arising from a vestibular depression with or without a ventral sulcus; with a posterior, often ventrally bent tail variable in shape, length and contents; with a single chloroplast bearing a pyrenoid not traversed by thylakoids. Nucleomorph positioned outside the pyrenoid. Periplast with discrete, hexagonal periplast areas in the main portion of the cell body; discrete periplast areas absent in the region of the tail.

Habitat: marine and freshwater.

Lectotype species: *Plagioselmis prolonga* Butcher ex Novarino, Lucas et Morrall.

Taxa of *Plagioselmis*

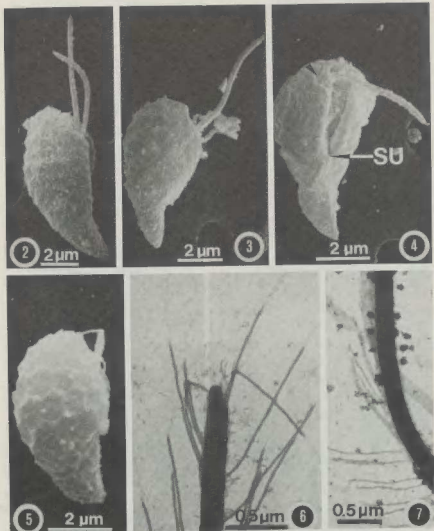
Plagioselmis prolonga Butcher ex Novarino, Lucas et Morrall sp. nov.

(Figs 1 - 18)

Synonym: *Plagioselmis prolonga* Butcher 1967, *Fishery Invest. Lond., Ser. IV:* 18, pl. I fig. 9, pl. XIV fig. 2, typ. non desig.; Hill 1992, p. 165, figs 1 A - P; Kuylenstierna & Karlson 1994, p. 22, figs 8a, b.

Allied taxa: *Plagioselmis prolonga* forma *japonica* Throndsen 1983, p. 5, fig. 11; *Plagioselmis* sp. 'B' Throndsen 1983, p. 5, figs 9, 10; *Plagioselmis punctata* Butcher 1967, p. 19, pl. I fig. 10, pl. XIV fig. 3; *Chroomonas* sp. Andreoli *et al.* 1986, figs 1 - 6; *Chroomonas* sp. Bisalputra *et al.* 1973, fig. 14; *Cryptomonas* sp. Booth *et al.* 1982, fig. 21.

Description: Lugol-fixed, non critical point-dried cells uncompressed, on average 8.6 µm long (SD = 1.15, n = 39) and 4.7 µm thick (SD = 0.77, n = 39). Flagella subequal, 1/2 - 2/2 the cell length. Ventral sulcus present. Tail 1/7 - 1/3 the cell length, usually acute, conical or laterally flattened, containing a mitochondrial profile. Chloroplast dorsal, c-shaped, with ventral margins not extending deeply into the ventral region of the cell, containing phycoerythrin $\bar{1}$ (535 - 545 nm) as principal accessory pigment. Pyrenoid anterior, small, with a thin starch sheath. Nucleus central. Partially overlapping scales ca. 80 nm in diameter present on the external face of the plasma membrane. Side of the periplast areas

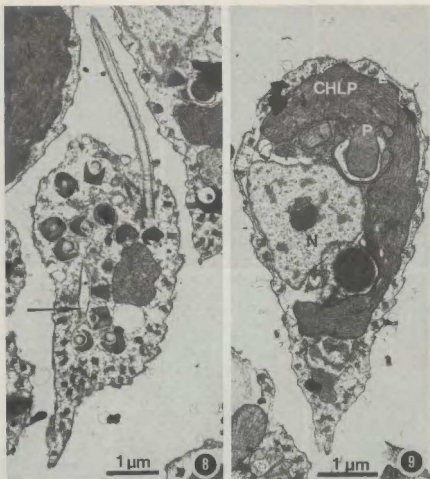


Figs 2 - 7. *Plagioselmis prolonga* PLY 172a, SEM, pre-glutaraldehyde / glutaraldehyde / osmium / CPD, and TEM, uranyl-stained whole-mounts. Fig. 2. Lateral view. Fig. 3. Dorso-lateral view, showing hexagonal periplast areas on the main portion of the cell body only. Fig. 4. Ventral view; note the position of the vestibular depression (arrowhead) with respect to the ventral sulcus (SU). Fig. 5. Dorsal view; note the hexagonal periplast areas on the main portion of the cell body only. Fig. 6. Whole-mount of the dorsal flagellum; note the bilateral array of tubular hairs. Fig. 7. Whole-mount of the ventral flagellum; note the unilateral array of tubular hairs.

on average $0.39 \mu\text{m}$ long ($SD = 0.087$, $n = 30$), in chemically fixed, dehydrated and critical point-dried cells examined by scanning electron microscopy.

Habitat: marine.

Lectotype: Butcher 1967, pl. I fig. 9.



Figs 8, 9. *Plagioselmis prolonga* PLY 172a. TEM. Fig. 8. Longitudinal section showing the position of the flagella with respect to the gullet (arrow). Fig. 9. Longitudinal section showing chloroplast (CHLP), pyrenoid (P), and nucleus (N).

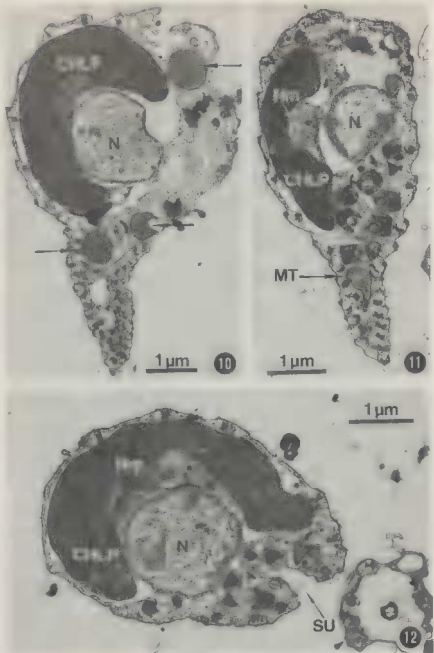
Plagioselmis prolonga var. *nordica* Novarino, Lucas et Morrall var. nov.

(Figs 19, 20)

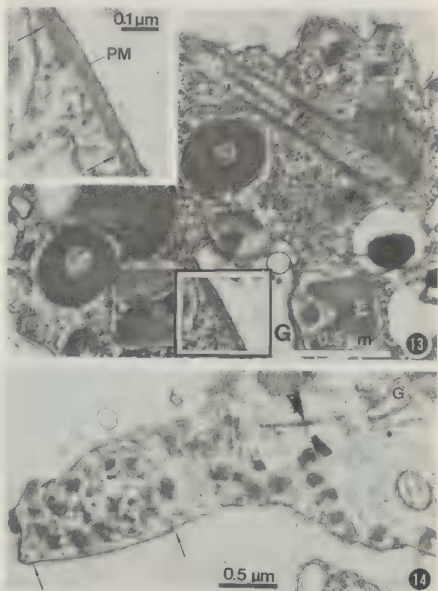
Synonym: *Plagioselmis* sp. Novarino 1991b, p. 602, figs 3, 4.

Allied taxa: *Plagioselmis* sp. 'A' Thronsen 1983, p. 5, figs 7, 8. *Cryptomonas acuta* sensu Chang 1983, fig. 7A.

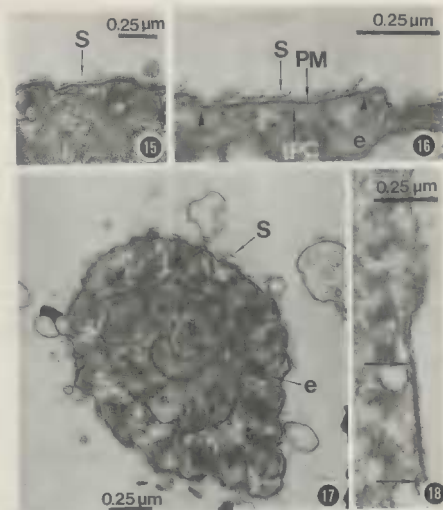
Diagnosis: *Cellulae sine sulco, non compressae, in media 5.8 µm longae (SD = 0.8, n = 6) et 2.6 µm crassae (SD = 0.47, n = 3), in speciminibus fixatis, dehydratis et ad punctum criticale exsiccatis; flagellis circiter 4/3 longitudinis cellulae; areis periplasti in media 0.31 µm latis (SD = 0.041, n = 15) in speciminibus fixatis, dehydratis et ad*



Figs 10 - 12. *Plagioselmis prolunga* PLY 172a, TEM. Fig. 10. Longitudinal section showing chloroplast (CHLP), nucleus (N), and circular mitochondrial profiles (arrows). Fig. 11. Longitudinal section showing chloroplast (CHLP), nucleus (N), nucleomorph (Nm), and mitochondrial profile (MT) inside the tail. Fig. 12. Median transverse section showing chloroplast (CHLP), nucleus (N), nucleomorph (Nm) and ventral sulcus (SU).



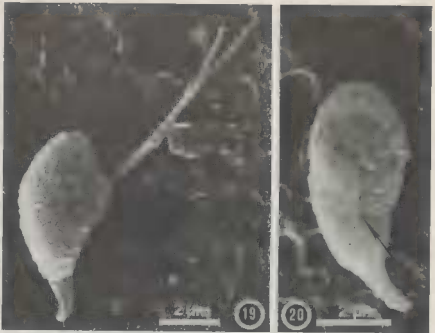
Figs 13, 14. *Plagioselmis prolunga* PLY 172a, TEM. Fig. 13. Longitudinal section in the anterior region of the cell; in the inset, which is $\times 2$ photographic enlargement of the boxed region of the gullet (G), note the electron-opaque band underneath the membrane (PM) on one side of the gullet only (arrows); E = large ejectosome vesicle. Fig. 14. Longitudinal section showing that the periplast of the tail (arrows) is not subdivided into discrete areas; note also the (presumably fibrous) band extending from the gullet (G) towards the tail (arrowhead).



Figs 15 - 18. *Plagioselmis protonga* PLY 172a, TEM. Figs 15, 16. Sections of the perioplast on the main portion of the cell body, showing a single layer of scales (S) on the external face of the plasma membrane (PM), and an electron-dense internal component (IPC), which is subdivided into discrete areas (arrowheads); e = small ejectosome vesicles. Fig. 17. Transverse section of a tail, showing a large mitochondrial profile; note external scales (S) and small ejectosome vesicles (e) bulging towards the cell surface. Fig. 18. Longitudinal section of a tail, showing a continuous internal perioplast layer (arrows); note that external scales are absent.

punctum criticale exsiccatis. Cauda circiter 1/5 longitudinis cellulae. Holotypus: Figura 19.

Cells without a sulcus, uncompressed, on average 5.8 μm long (SD = 0.8, n = 6) and 2.6 μm thick (SD = 0.47, n = 3), in chemically fixed, dehydrated and critical point-dried specimens examined by scanning electron microscopy; flagella about 4/3 the cell



Figs 19, 20. *Plagioselmis protonga* var. *nordica*. North Sea, SEM, Lugol / cold osmium / CPD. Fig. 19. (holotype). Lateral view. Fig. 20. Ventral view; the ventral fold is interpreted as a shrinkage artefact.

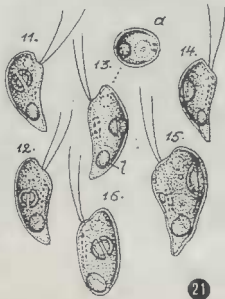


Fig. 21. Reproductions of Skuja's (1948) illustrations of *Rhodomonas minuta* var. *nannoplanctica*, twice the size of the originals.

length; side of the periplast areas on average 0.31 μm long (SD = 0.041, n = 15), in chemically fixed, dehydrated and critical point-dried cells examined by scanning electron microscopy. Tail about 1/5 the cell length.

Holotype: Fig. 19, from a plankton sample from the southern North Sea, collected on 8/8/1988 at 4 m depth from station BG during cruise no. 33 of the U. K. Natural Environment Research Council (NERC) North Sea Community Project 1988/89.

***Plagioselmis nannoplanctica* (Skuja) Novarino, Lucas et Morrall comb.
et stat. nov.** (Figs 21 - 26)

Basionym: *Rhodomonas minuta* var. *nannoplanctica* Skuja 1948, *Symbolae Botanicae Upsalienses*, 9: 347, pl. XXXVII, figs 11 - 15 (excl. fig. 16); Kristiansen 1959, p. 22, pl. 5, figs 4, 6; Lund 1962, figs 1-41; Garcia de Emiliani 1973, p. 125, fig. 16.27; Armenogol *et al.* 1975, p. 13, fig. 2 B; Munawar & Bistricki 1979, fig. 9 (bottom cell); Sommer 1982, fig. 2 RH M; Caljon 1987, p. 40, pl. 3, fig. 26 (excl. figs 27-30); Dokuli 1988, figs 1.3, 1.4.

Synonyms: *Rhodomonas lacustris* var. *nannoplanctica* (Skuja) Javornicky 1976, p. 103, pl. 24, figs 1-3, 6-8, 10, excl. figs 4, 5, 9, 11, 12 (obligate synonym). *Rhodomonas minuta* sensu Munawar & Bistricki 1979, fig. 11, et sensu Willén *et al.* 1980, fig. 9, non *Rhodomonas minuta* Skuja 1948, p. 346, pl. XXXVII, figs 8-10. *Rhodomonas lacustris* sensu Klaveness 1981, figs 1-15.

Allied taxa: *Rhodomonas pusilla* Bachmann 1923, p. 165, fig. 5. *Cryptomonas curvara* [sic] Guseva 1936, p. 223, fig. 4. *Rhodomonas pusilla* (Bachmann) Javornicky 1967, p. 50, pl. 4, figs 1-6; *Chroomonas pusilla* (Bachmann) Happey-Wood 1976, p. 356. *Rhodomonas minuta* (var. *nannoplanctica*?) sensu Munawar & Bistricki 1979, fig. 14. *Chroomonas acuta* sensu Kugrens & Lee 1988, p. 386, figs 2 et seq..

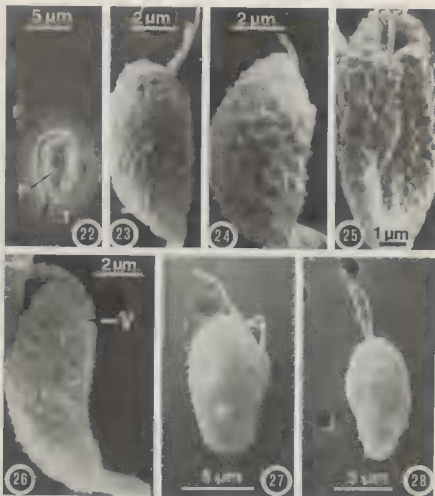
Description: Cells uncompressed, on average 9.3 μm long (SD = 1.20, n = 30), 4.1 μm thick (SD = 0.24, n = 19), and 4.4 μm wide (SD = 0.47, n = 11), in chemically fixed, dehydrated, and critical point-dried specimens examined by scanning electron microscopy. Flagella unequal, long flagellum 3/4 the cell length, short flagellum 1/2 the cell length. Sulcus absent. Tail 1/10 - 1/5 the cell length, usually acute, conical, cylindrical, or blade-like, containing a refringent inclusion ('leucosin granule') not delimited by membranes. Chloroplast dorsal, with ventral margins extending deeply into the ventral region of the cell, containing phycoerythrin I (540 - 545 nm). Pyrenoid central, large, with a thick starch sheath made up of two hemispherical halves. Nucleus posterior. Body scales absent. Side of the periplast areas on average 0.46 μm long (SD = 0.053, n = 30), in chemically fixed, dehydrated, and critical point-dried specimens examined by scanning electron microscopy.

Habitat: freshwater.

Lectotype: Skuja 1948, pl. XXXVII, fig. 13.

OBSERVATIONS

Morphometric features of the taxa of *Plagioselmis* examined here are summarised in Tables I and II. As reported elsewhere for other cryptomonads (Novarino, 1991a, b),



Figs 22 - 28. *Plagioselmis nannoplanctica* DK N750301 and an *Isoselmis*'-like cryptomonad. Figs 22 - 26. *Plagioselmis nannoplanctica* DK N750301. Fig. 22. Lugol, phase-contrast LM; F = flagella, P = pyrenoid, T = tail. Figs 23 - 26. SEM, glutaraldehyde / osmium / CPD. Fig. 23. Lateral view; tail straight. Fig. 24. Lateral view; tail conical and ventrally bent. Fig. 25. Ventral view of a cell showing obvious signs of shrinkage; the long ventral fold is interpreted as a shrinkage artefact. Fig. 26. Ventro-lateral view; tail long, cylindrical, and ventrally bent. Note also the vestibular depression (V) and the absence of a ventral fold. Figs 27, 28. An *Isoselmis*'-like cryptomonad (strain Y/C), SEM, glutaraldehyde / osmium / CPD, in lateral (Fig. 27) and dorsal (Fig. 28) views.

during specimen preparation for SEM cells shrink by a variable amount, whose significance can be tested statistically (Tab. II).

In culture *P. prolonga* and *P. nannoplanctica* behave in a very similar way. Both species are difficult to maintain and must be subcultured frequently (every 2 weeks) in order to minimise the risk that the cells die suddenly. Growth is very slow under the cultural conditions used here. Swimming is usually rapid, but cells under stress may not swim at

all; instead, they may be found rotating rapidly about the perilateral axis, with no net translational movement.

Table I - Morphometric features of three taxa of *Plagioselmis* prepared for SEM according to the glutaraldehyde/osmium/CPD schedule (*P. prolonga*, *P. nanoplancytica*) or the Lugol/osmium/CPD schedule (*P. prolonga* var. *nordica*). Values are given as mean \pm standard deviation, with the number of observations in brackets. CL = cell length, CT = cell thickness (dorso-ventral), CW = cell width (perilateral), PAs = size of the periplast areas (length of the hexagon side).

Taxon	CL (μm)	CT (μm)	CW (μm)	PAs (μm)
<i>P. prolonga</i> PLY 172a	7.3 \pm 0.87 (30)	3.4 \pm 0.35 (13)	3.4 \pm 0.24 (16)	0.39 \pm 0.087 (30)
<i>P. prolonga</i> var. <i>nordica</i> (*)	5.8 \pm 0.80 (6)	2.6 \pm 0.47 (3)	2.8 \pm 0.26 (3)	0.31 \pm 0.041 (15)
<i>P. nanoplancytica</i> DK N750301	9.3 \pm 1.20 (30)	4.1 \pm 0.24 (19)	4.4 \pm 0.47 (11)	0.46 \pm 0.053 (30)

(*) data from Novarino (1991b)

Table II - Comparisons of cell length (CL) and cell thickness (dorso-ventral)(CT), measured with the LM (Lugol-fixed cells) and SEM (cells prepared according to the glutaraldehyde/osmium/CPD schedule) in 2 species of *Plagioselmis*. DF = degrees of freedom.

Species and parameter	Mean value in LM (μm)	Mean value in SEM (μm)	Difference (LM - SEM)	t, DF, p
<i>P. prolonga</i> , CL	8.6	7.3	1.3 (15.1%)	4.999 [67]; p<0.001
<i>P. prolonga</i> , CL	4.7	3.5	1.2 (25.5%)	5.795 [50]; p<0.001
<i>P. nanoplancytica</i> , CL	10.5 (*)	9.3	1.2 (11.4%)	(**)
<i>P. nanoplancytica</i> , CT	5.7 (*)	4.1	1.6 (28.1%)	(**)

(*) data from Klaveness (1981)

(**) pooled t-statistic not calculated owing to insufficient data.

In the LM the salient features of *Plagioselmis prolonga* are the anterior pyrenoid, the subequal flagella, and especially the shape of the cells (Fig. 1). The anterior end is broadly rounded, whereas the posterior one is acute. Careful examination shows that the posterior end is hyaline and usually curved in the ventral direction (Fig. 1). The posterior end will be referred to here as the 'tail'. In the SEM the cell shape and the appearance of the flagella match closely those observed with the LM (Figs 25). Cells are covered with distinctly hexagonal periplast areas (PAs) (Figs 3, 5), except in the region of the tail, which lacks PAs (Fig. 3). The tail is usually conical in shape, although a blade-like (laterally flattened) form may also occur (Fig. 4). The flagella arise from a small, apical or subapical vestibular depression, which is displaced laterally towards one side of the cell (Fig. 4). Towards the opposite side (i.e., along the median longitudinal axis of the cell), the vestibular depression leads into a wide ventral groove extending roughly halfway along the cell length

(Fig. 4). A total of 40 cells were examined where the ventral face was clearly visible. Since a groove was observed in all of these, and was not characteristically associated with obvious signs of cell shrinkage, it is interpreted as a true, non-artefactual cellular feature. In order to avoid any possible confusion, due to the fact that the term 'furrow' may have been used indiscriminately for artefactual and non-artefactual grooves alike (see Novarino 1991b), the groove of *P. prolonga* will be referred to here as a 'sulcus' sensu Novarino (1991b).

In TEM whole-mounts the dorsal flagellum shows 2 rows of tubular hairs, whereas the ventral one has a single row (Figs 6, 7). In addition, two rows of much shorter fibrillar hairs appear to be present on the dorsal flagellum (Fig. 6; see also Morrall, 1980). Sections confirm the presence of a sulcus (Fig. 12), and suggest that it extends internally into a closed gullet (Fig. 8). On one side of the gullet, the plasma membrane is lined internally with an electron-dense, presumably fibrous band (Fig. 13), which appears to extend towards and possibly reach the tail (Fig. 14). On the other side of the gullet this band is absent, and the limiting membranes of the large ejectosome vesicles may come into close contact with the gullet membrane (Fig. 13). The position of the flagellar bases appears to be displaced relative to the gullet (Figs 8, 13), supporting the SEM observations.

The chloroplast of *P. prolonga* appears c-shaped both in longitudinal (Figs 9 - 11) and transverse (Fig. 12) sections. It does not extend into the tail (Figs 9 - 11), and its ventral margins do not extend deeply into the ventral region of the cell (Fig. 12). In the anterior region it bears a small pyrenoid not traversed by thylakoids and surrounded by a thin starch sheath (Fig. 9). The chloroplast surrounds a central nucleus (Figs 9 - 12). Owing to the fact that the phycobilin extract shows a broad absorbance peak in the region 535 - 545 nm, the chloroplast appears to contain phycoerythrin I (*cr*-phycoerythrin 545 in the sense of Hill & Rowan 1989) as principal accessory pigment.

In the periplastidial compartment there is a single nucleomorph, closely appressed to the nucleus (Figs 11, 12). Since the nucleomorph is positioned outside the pyrenoid, *P. prolonga* belongs to the order Cryptomonadales Novarino et Lucas (Novarino & Lucas, 1993b) (non Cryptomonadales Pascher nec Cryptomonadales auctorum). Mitochondrial profiles are usually circular (Fig. 10), and one profile always appears to be present inside the tail (Figs 11, 17).

In sections the periplast of *P. prolonga* is made up of an electron-dense component (IPC) on the internal face of the plasma membrane (PM) (Fig. 16). The IPC forms discrete segments, the size of which is comparable to that of the PAs seen with the SEM (Figs 15, 16). Small ejectosome vesicles bulge towards the surface between adjacent PAs (Figs 15, 16). Outside the plasma membrane there is a layer of partially overlapping scales ca. 80 nm in diameter (Figs 15 - 17). The IPC of the tail appears to be sheet-like, i.e. not composed of discrete PAs (Figs 14, 18), although at times the numerous small ejectosome vesicles which bulge towards the surface may give a false impression that the tail periplast is made up of discrete PAs (Fig. 17). Tails have been observed with or without external 80-nm scales (compare Figs 17 and 18).

Plagioselmis prolonga var. *nordica* (Figs 19, 20) is smaller than var. *prolonga*, has longer flagella, and the PAs are slightly smaller. Fig. 20 shows that the ventral cell face may bear a narrow groove. However, the fact that the groove is associated with obvious signs of cell shrinkage strongly suggests that it is a shrinkage artefact.

Apart from the freshwater habitat, *P. nannoplanctica* (Figs 21 - 26) is superficially similar to *P. prolonga*. However the much larger pyrenoid tends to occur in the central region of the cell (Fig. 22), and is covered by a much thicker starch sheath composed of two

halves (Klaveness, 1981, figs 9, 14, 15). The flagella are unequal (Fig. 22). The tail is more variable in length and shape, ranging from acute-conical (Figs 23, 24) to blade-like or cylindrical (Fig. 26). The small circular vestibular depression from which the flagella arise may lead to a long fold on the ventral cell face (Fig. 25). This is regarded here as a shrinkage artefact, owing to the fact that cells lacking obvious signs of shrinkage also lack a ventral fold (Fig. 26). Information available from the TEM study by Klaveness (1981) shows that there are other differences between *P. nannoplantica* and *P. prolonga*; these are summarised in Tab. III.

DISCUSSION

Strain PLY 172a, identified by its isolator as belonging to *Plagioselmis punctata*, is assigned here to *P. prolonga*. Although the values of cell size are smaller than those given by Butcher (1967) for the latter species, this strain possesses certain key features which warrant its assignment to *P. prolonga*, i.e. the size and position of the pyrenoid, and the usually acute posterior tail. We support Chrétiennot-Dinet's (1990) designation of *Plagioselmis prolonga* as type of the genus *Plagioselmis*. This species should be preferred to *P. punctata* as the type of the genus owing to some contradictions contained in the original description of *P. punctata*. This is described in the Latin diagnosis (Butcher, 1967, p. 19) as having an anterior pyrenoid, but the English description mentions a central pyrenoid, which is also figured in one of the original illustrations (Butcher, 1967, pl. 1, fig. 10 left).

The presence of a posterior tail lacking the discrete periplast areas found on the main portion of the cell body, is considered here as a diagnostic feature of the genus *Plagioselmis*. This is in line with current views that major differences in periplast structure are taxonomically significant at the generic level. Minor differences - for instance, the structure of the external periplast component - appear to be significant at or below the specific level (Novarino, 1991a).

Kugrens & Lee (1988) reported that the tail acts as a 'mating structure' between gametes during sexual reproduction. In cultures of *Plagioselmis prolonga* and *P. nannoplantica* observed in different growth phases over long periods of time, no evidence of sexual reproduction has been found.

The presence of a tail typical of *Plagioselmis* in several cryptomonads illustrated with the SEM in the literature, has led us to include these as synonyms or 'allied taxa' of some of the taxa described here. The tail typical of *Plagioselmis* is also present in a freshwater cryptomonad (strain DK N 750301), named *Rhodomonas lacustris* sensu Javornicky (1976) by Klaveness (1981). This is a common and ecologically important cryptomonad which, contrary to the views of Javornicky (1976), is most often referred to as *Rhodomonas minuta* var. *nannoplantica* Skuja (Reynolds, 1978, and references in Stewart & Wetzel, 1986). In the original description of that variety by Skuja (1948, p. 347) there are detailed comments on the tail and its refringent granule ('Leukosinballe'), which are absent in *Rhodomonas minuta* var. *minuta* Skuja (1948, p. 346). A comparison with strain DK N 750301 shows that this strain can effectively be identified as *Rhodomonas minuta* var. *nannoplantica*. However, our observations show that strain DK N 750301 possesses the distinctive features of the genus *Plagioselmis*. It is necessary, therefore, to recombine Skuja's *Rhodomonas minuta* var. *nannoplantica* under *Plagioselmis*. In doing so the rank of Skuja's variety is raised to that of a species, since there are considerable differences

between it and *P. prolunga* (Tab. III). The most obvious difference is given by the freshwater habitat of *P. nannoplanctica*. In this respect it is interesting to note that the generic name *Plagioselmis* has already been used in the ecological literature for a freshwater bloom-forming cryptomonad (Nishijima *et al.*, 1990, no figs)

Table III - A comparison of some non-morphometric characters in three taxa of *Plagioselmis*. CVM = chloroplast ventral margin, F = flagella, H = habitat, LG = 'leucosin granule', MT = mitochondrion, N = nucleus, P = pyrenoid, S = body scales, SU = sulcus, T = tail. Missing data are listed as '?', absence of feature as '0'.

Taxon	T	SU	F	S	P	N	CVM	H
<i>P. prolunga</i> PLY 172a	with MT	+	subequal 1/2-2/2 cell length	+	anterior	central	not extending deeply into ventral cell region	marine
<i>P. prolunga</i> var. <i>nordica</i>	?	0	subequal 4/3 cell length	?	anterior	?	?	marine
<i>P. nannoplanctica</i> DK N750301 (*)	with LG	■	unequal (3/4 and 1/2 cell length)	0	central	posterior	extending deeply into ventral cell region	fresh water

Under the International Code of Botanical Nomenclature (ICBN), the type of a new combination is the type of the basionym (art. 7.12). The holotype of the basionym of *Plagioselmis nannoplanctica* is unknown since Skuja (1948) did not designate it. Although this does not contravene the requirements of the ICBN at Skuja's time of writing (art. 37.1), in order to adequately typify *Plagioselmis nannoplanctica* a lectotype chosen from among Skuja's original illustrations of *Rhodomonas minuta* var. *nannoplanctica* is proposed (Skuja, 1948, pl. XXXVII, fig. 13; reproduced here in Fig. 21 along with Skuja's other illustrations).

Arvola *et al.* (1991, figs 5, 6), have illustrated with the SEM a cryptomonad from the Culture Collection of Algae and Protozoa, U. K. (strain no. 995/3), identified as *Rhodomonas minuta* var. *nannoplanctica*. It is unclear whether or not that strain can be assigned to the genus *Plagioselmis*, since it is unknown whether the tail possesses a sheet-like periplast or a periplast subdivided into discrete areas. Similarly, a cryptomonad illustrated with the SEM and identified as *Cryptomonas cryophila* Taylor *et Lee* by McMinn & Hodgson (1993, fig. 5) shows an overall resemblance to *Plagioselmis prolunga*, but the periplast type in the region of the tail is also unknown. In contrast, a cryptomonad identified as *Rhodomonas lacustris* by Basualto (1992, p. 27, figs 1, 4-6) was described as having hexagonal periplast areas on the main portion of the cell body, but no such areas on the posterior tail. Therefore, it can be considered as a member of the genus *Plagioselmis*, and probably a new taxon since it combines some of the features typical of *P. prolunga* var. *prolonga* (presence of a non-artefactual sulcus and flagella arising from a laterally displaced vestibule: see the SEM micrograph of Basualto, 1992, fig. 6, and p. 29) with other features characteristic of *P. nannoplanctica* (presence of a refringent inclusion inside the tail and a large pyrenoid: see Basualto, 1992, p. 28).

The tail of *Plagioselmis* may have been observed as early ■ in the 1920s or 1930s in some freshwater cryptomonads assigned by their authors to the genus *Cryptomonas*

Ehrenberg, e.g. *Cryptomonas caudata* Massart (1920), *C. pusilla* Bachmann (1923), and *C. curvata* [sic] Guseva (1936). The names of those species, together with some later recombinations, are considered here as names of taxa allied to *Plagioselmis nannoplantica*, but it is also possible that some or all of those species effectively correspond to *P. nannoplantica*. If this were indeed to be the case, then the correct (earliest available) basionym for the species bearing the name *Plagioselmis nannoplantica* would have to be chosen from among *Cryptomonas caudata*, *C. pusilla*, and *C. curvata*. However, owing to the insufficient descriptions of *Cryptomonas caudata*, *C. pusilla*, and *C. curvata*, the basionym *nannoplantica* is retained here. Skuja's diagnosis of *Rhodomonas minuta* var. *nannoplantica* contains an unequivocal reference to the posterior tail typical of *Plagioselmis* (*parte posteriore acutius attenuata deorsum plerumque plus incurva*: Skuja, 1948, p. 347). In addition, Skuja's illustrations (reproduced here, Fig. 21) show ■ large pyrenoid bearing ■ starch sheath composed of two halves, as is also the case with strain DK N750301 on which our description of *Plagioselmis nannoplantica* is based (Klaveness, 1981, figs 9, 14, 15).

In the early literature several other cryptomonads have been described which appear to possess a posterior tail and, therefore, are possible members of the genus *Plagioselmis*. Most are 'red' (phycoerythrin-containing); some examples can be found in Schiller (1957), e.g. *Cryptomonas vindobonensis* Schiller on p. 36, pl. XII figs 54 a - c. *Chroomonas acuta* Utermöhl (1925, p. 399, fig. 34), on the other hand, is ■ example of a tail-bearing cryptomonad described as being olive-green or 'dirty green' in colour; ■ such, it probably contains phycocyanin. (Cells of *Chroomonas acuta* sensu Kugrens & Lee (1988) were described as being golden-brown in colour. This may reflect the presence of phycoerythrin, and therefore suggests that *Chroomonas acuta* sensu Kugrens & Lee is closely allied to *Plagioselmis nannoplantica*). Hill (1991) listed *Chroomonas acuta* as a synonym of *Komma caudata* (Geitler) Hill, and provided an SEM micrograph (Hill, 1991, fig. 28) showing that the tail of *Komma caudata* bears hexagonal periplast areas, as does the main portion of the cell body. However, SEM micrographs of *Chroomonas acuta* (Hickel, 1975, fig. 1; Cronberg, 1982, fig. 173), show that the hexagonal periplast areas of the cell body do not extend onto the tail. This supports the idea that *Chroomonas acuta* and *Komma caudata* are distinct, non-congeneric species, and suggests that *C. acuta* may belong to the genus *Plagioselmis*. If *Plagioselmis* effectively includes both phycoerythrin- and phycocyanin-containing species, it would be unlike most cryptomonad genera. The only genus known to include both phycoerythrin- and phycocyanin-containing species is *Hemiselmis* Parke, which is subdivided into two subgenera based on the phycobilin type (Butcher 1967; Hill & Rowan 1989; Novarino & Lucas 1993b).

In redescribing the genus *Plagioselmis* an attempt has been made to establish which characters ■ taxonomically significant at the generic level, and which ones can be used for delimiting species and varieties. Characters at and below the species level (Tab. III) include the 80-nm scales covering the cell body of *P. prolunga*. Scales of that size are unusual since they are only about 1/2 the size found in other cryptomonad genera. However, they do not seem to occur in species of *Plagioselmis* other than *P. prolunga* and, therefore, they do not appear to be taxonomically significant at the generic level.

The set of specific characters used in the genus *Plagioselmis* is comparable to that used in other genera of cryptomonads (Novarino, 1991a, b; Novarino & Lucas, 1993a), since it includes the size of the periplast areas and the presence of a sulcus. These characters appear of general usefulness for delimiting cryptomonad species. Some of the specific characters in the genus *Plagioselmis* are visible with the light microscope, i.e. relative fla-

gellar length and the position of the pyrenoid. Those characters could be useful during routine identifications of specimens in natural samples. If other taxonomically important characters in the Cryptophyceae may be observed with the light microscope, as suggested elsewhere for the periplast areas and the nucleomorph (Novarino, 1993), then there is great potential in trying to correlate light and electron microscopical observations for taxonomic and identification purposes.

The status of the genus *Isoselmis* is unclear. This was described by Butcher (1967, p. 19) based on a single species, *I. obconica* Butcher (1967, p. 20, pl. I fig. 11, pl. XII fig. 1, pl. XIV fig. 4). *Isoselmis* was distinguished from *Plagioselmis* 'with some hesitation' based on the behaviour of the flagella and the number of large ejectosomes. Both of these characters are difficult to observe with certainty, the behaviour of the flagella in particular owing to the cells' rapid swimming. Specimens which could be identified by light microscopy as possible members of the genus *Isoselmis* (Fig. 29) were isolated from aquarium tanks at the School of Ocean Sciences, Menai Bridge, U. K.. A posterior refringent granule was a prominent feature of all of the cells examined, as described for *I. obconica*. In the SEM (Figs 27, 28) the periplast appeared sheet-like, as in the 'diplomorphs' of the genus *Proteomonas* Hill et Wetherbee (Hill & Wetherbee, 1986; Novarino, 1991b). It is impossible to know with certainty if the specimens effectively belong to the genus *Isoselmis*, since the original culture of *I. obconica* (PLY no. 9) is no longer available, and no other strains bearing the generic name *Isoselmis* are available from culture collections. As is often the case with names of insufficiently characterized taxa on which little information is available (Jeffrey, 1977), it appears that the generic name *Isoselmis* may represent a nomen dubium which cannot be applied to any taxon.

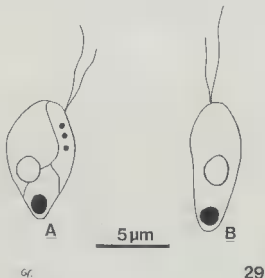


Fig. 29. An *Isoselmis*-like cryptomonad (strain Y/C), LM, in lateral (a) and dorsal (b) views.

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